Journal of Foraminiferal Research, v. 32, no. 1, p. 68–93, January 2002

FORAMINIFERAL DENSITIES OVER FIVE YEARS IN THE INDIAN RIVER LAGOON, FLORIDA: A MODEL OF PULSATING PATCHES

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ABSTRACT

Densities of 5 taxa along with 7 environmental variables were measured monthly with 4 replicates at each of 3 stations over a period of 5 years. The 720 observations of density for each taxon were analyzed by General Linear Models with density as the dependent variable. Differences among stations, years, seasons and their interactions are all significant. When treated as covariates environmental variables contributed little to explaining the observed variability in densities. However, the observed densities of the taxa are highly correlated and when a single taxon is treated as a covariate most of the variability in the density of a related taxon is explained. There are no significant differences among replicates (taken within a square meter) or their interactions. Consequently, the biotic or abiotic factor(s), although unknown, responsible for the simultaneous density variation of the taxa operate on a relatively small spatial scale. Based on these observations and previous studies, we propose a model wherein individual foraminifers are spatially distributed as a heterogeneous continuum forming patches with different densities that are only meters apart; reproduction is asynchronous causing pulsating patches that vary in space and time. Thus, we would expect significant differences among stations, years, seasons and their interaction. At the same time, no long-term increase or decrease in density for any of the taxa is observed. Evidently, long-term stability is achieved through considerable short-term variability in space and time. Although observations at a single station are not indicative of a larger area at any particular time, the concept of pulsating patches indicates that observations at a station will in the long-term give an assessment of a larger area.

INTRODUCTION

The Indian River Lagoon (IRL) is a long (140 Km), narrow (1 Km) estuary located behind a barrier island off the central Atlantic coast of Florida. In the central portion of the IRL, during our 5 years of sampling, water temperatures ranged from 15 to 37° C, averaging 26° C, and salinities from 18 to 40 ‰, averaging 28 ‰. The bottom is composed of 95% quartz sand. The IRL is species rich and has been the site of extensive ecological studies on a wide range of organisms (Authors, Bulletin of Marine Science, v. 57, no. 1, 1995).

The distribution and systematics of the foraminifera dwelling in the IRL was documented by Buzas and Severin (1982). The species richness of the 94 identified species increased from north to south and canonical variate analysis of the 15 most abundant species discriminated the four inlets from the estuary while arranging the entire ensemble into a north-south pattern. At a centrally located station, Buzas (1978, 1982) demonstrated through caging experiments that the density of foraminifera is severely limited by predation and that a wide variety of invertebrates and vertebrates ingest foraminifera (Buzas and Carle, 1979). Living (stained) foraminifera typically live to a depth of about 6 cm within the sandy substrate of the IRL (Buzas, 1977). Field experiments also demonstrated that the foraminifera colonize newly introduced azoic sand within a few weeks, indicating rapid dispersal capabilities (Buzas, 1993).

Seasonality in foraminiferal densities has interested researchers for many years (for example, Myers, 1943; Walton, 1955). Studies carried out over the period of a year or less have tacitly assumed that the periodicity established over one year will apply to another and that the observed seasonal pattern extended over a large area (for example, Buzas, 1965). More recent research has indicated that this is not the case. In the IRL, two stations about 10 m apart, one in seagrass and the other on bare sand, were each sampled with four replicates every fortnight over a period of 10 months. A general linear model used for statistical analysis indicated no overall difference, but each station exhibited a different periodicity (Buzas and Severin, 1993). A few foraminiferal studies have carried out monthly sampling over a period of two to two and one half years (see, Murray and Alve, 2000, and references therein). These studies indicate that usually there are differences between years and seasons, and that the seasonality present in one year may not be present in another. Indeed, one station may exhibit seasonal periodicity while a nearby station may not. The studies of Buzas (1969), Schafer (1971) and Murray and Alve (2000) have pointed out that a major difficulty with most foraminiferal studies is the lack of replicate sampling (see, Hayek and Buzas, 1997, for a discussion on the importance of replicate sampling). At a single station in the IRL monthly samples with four replicates at each sampling time were carried out over a four year period from 1993–1996. Analyses of these data (Buzas and Hayek, 2000) indicate significant differences in foraminiferal densities among years, seasons and their interaction. The significance of the interaction hypotheses indicates that not only do densities differ among years and with seasons, but they differ differently with the seasons in different years. In other words, every possible variation occurs. At this same IRL station, data were available from the controls of the experiments cited above (mostly summer) extending to 1977. In the most extensive long-term replicated study available to date, analyses of the 20 year period from 1977–1996 indicate significant differences among years, but no overall trend of increasing

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or decreasing density. Thus, we observe great variability among years achieving long-term equilibrium.

In the present study, we analyze data from samples collected at three stations in the central IRL with four replicates at each monthly sampling over a period of five years. Five taxa of living foraminifera (rose bengal-stained) were enumerated in each sediment sample. At each sampling time, 6 environmental variables were also measured. The full factorial design of the observations allows for analysis by a general linear model with hypotheses for testing for differences among years, stations, their interactions and environmental variables. We examine the contribution of the variance components of the hypotheses and construct several models to examine our observations on foraminiferal densities.

METHODS

Field Sites and Sampling

The three stations sampled in this study are all located in the south-central part of the IRL between Vero Beach and Ft. Pierce, Fl. Centrally located between these cities, the Harbor Branch Oceanographic Foundation has two parallel east-west jetties extending into the IRL forming a ship channel. Station 1 was located between the jetties adjacent to the southern side of the ship channel in about 1 m of water, 27° 32.05′ N 80° 20.8′ W. Station 2 was located just south of the southernmost jetty, about 0.5 Km south of station 1 in about 1 m of water, 27° 31.8′ N 80° 20.8′ W. Station 3 was located about 5 Km south of station 2 adjacent to a recreational boat channel in about 1 m of water, 27° 29.2′ N 80° 18.2′ W. Station 3 is about 1 Km away from the Ft. Pierce inlet to the Atlantic Ocean. We have, then, station 1 located near a ship channel, station 3 near a boat channel, and station 2 in a pristine area. Sampling was carried out during the middle of each month from February, 1992 to January, 1997.

At each monthly sampling time, four replicates for foraminiferal analysis were collected within an area of about 1 m^2 by inserting plastic core liners of 3.5 cm diameter into the sediment. A fifth core was taken for sediment analysis. Immediately after obtaining the fifth core, a thermometer was inserted into the sediment contained therein to measure pore water temperature and a few drops of sea water were extracted to measure salinity by a refractometer. The pH of the pore water was measured by a pH meter equipped with a microprobe that was inserted into the sediment. During the last four years of the study O_2 was measured with an oxygen meter by dangling the probe just above the sediment water interface.

Laboratory Analysis

Upon return to the laboratory (within an hour), 5 ml of sediment was removed from the top of each of the four replicates. The sediment was washed over a 63 micron sieve and fixed in 95% ethyl alcohol. Before enumeration, samples were stained overnight with rose bengal (Walton, 1952; Murray and Bowser, 2000), washed over a 63 micron sieve, dried, concentrated by floating in sodium polytungstate and rewet. To insure recognition of living individuals, samples were counted while wet. The taxa counted were *Quinqueloculina* (mostly *Q. impressa* and *Q. seminula*), *Elphidium* (mostly *E. mexicanum* and *E. gunteri*), *Ammonia* (*A. beccarii*), *Bolivina* (mostly *B. striatula*) and *Ammobaculites* (*A. exiguus*).

For sediment analysis, 10 ml of sediment was extracted from the fifth core washed over a 63 micron sieve into Whatman 541 filter paper, dried in an oven at 60° C overnight, and then weighed. Weighing the fractions divided the sediment into sand and mud components. To obtain the amount of organic matter, the sediment was incinerated at 500° C for a minimum of 6 hours and weighed to determine the amount of loss.

Statistical Analysis

The purpose of the statistical analysis is to explain the observed differences in the densities of the taxa by stations, years, seasons, their interactions and environmental variables (Seal, 1964; Buzas, 1969). We constructed a general linear model (GLM) consisting of analysis of variance (ANOVA) components (stations, years, seasons, interactions) and regression components (environmental variables). The model written in matrix notation is $\mathbf{y} = \boldsymbol{\beta}\mathbf{X} + \mathbf{e}$, where $\mathbf{y}$ is the vector of observed densities, $\mathbf{X}$ is a matrix of instrumental variables (vectors for stations, years, seasons, interactions) and measured environmental variables, $\boldsymbol{\beta}$ a vector of coefficients calculated from $\mathbf{y}$ and $\mathbf{X}$ and $\mathbf{e}$ a vector of residuals or ‘‘errors’’ not accounted for by the model. All counts (numbers of individuals per 5 ml of sediment) were transformed to $\ln(y + 1)$ to promote equality of variances and normality. The GLM so constructed was compared to submodels by deleting components so the statistical significance of station differences, yearly differences, seasonal differences, their interactions and the environmental variables could be assessed using normal equations and the standard least squares technique.

In order to reduce the number of environmental variables entering the GLM, we first subjected the vector of densities, $\mathbf{y}$, to step-wise regression analysis with the environmental variables as predictors. We checked the results so obtained with individual and multiple regressions. In this way, we could usually reduce the six variables to two or three.

ENVIRONMENTAL VARIABLES

Water Temperature

The average water temperature at the three stations over the five year period (1992–1996) was 26° C. There was almost no difference in the observed temperature among stations. However, the years 1993 and 1996 were on the average a degree cooler and 1995 a degree warmer. As might be expected, the greatest variation in temperature is with seasons. Over a five year period the average temperatures by season were: 21° C, winter; 26° C, spring; 31° C, summer; 28° C, fall. The maximum temperature was 36° C and the minimum 16° C.

Salinity

The average salinity at all three stations over the five years of observation was 28‰. Unlike temperature, the av-

TABLE 1. General linear model for *Quinqueloculina*.*

Source	Sum of squares	df	Mean square	F ratio	P
Stations	544.38	2	272.19	241.41	0.00
Years	34.41	4	8.60	7.63	0.00
Seasons	79.13	3	26.38	23.40	0.00
Temperature	5.50	1	5.50	4.88	0.03
Mud	7.06	1	7.06	6.26	0.01
Stations × years	27.58	8	3.45	3.06	0.00
Years × seasons	55.16	12	4.60	4.08	0.00
Stations × seasons	49.38	6	8.23	7.30	0.00
Stations × years × seasons	132.14	24	5.51	4.88	0.00
Error	741.91	658	1.13		

* $N = 720$, $R^2 = 0.62$.

erage salinity was different among stations. At stations 1 and 2, salinity averaged 27‰, while at station 3, which is near the Ft. Pierce inlet, it was 31‰. The years 1994–1996 had an overall average salinity of 28‰; however, in 1992, the salinity averaged 29‰, and in 1993, 30‰. Seasonally, spring had the highest average of 30‰ and fall the lowest with 27‰. In 1996 at station 1 a spring minimum of 18‰ was recorded and at the same station in the spring of 1992 a maximum of 40‰ was recorded.

pH

The average pH varied only slightly among stations during the five years of observation. At station 1 the average was 7.5, at station 2, 7.6 and at station 3, 7.4. Similarly, the average pH varied only between 7.4 and 7.6 during years with 1993 being highest and 1996 the lowest. Seasonally, there was even less variation with winter averaging 7.4 and the remaining three seasons, 7.5. In 1996 a minimum of 6.0 and a maximum of 8.5 were recorded in the spring at station 2. Recordings of below 7.0 were observed only 6 times and they were scattered among stations, years and seasons.

SAND

The average weight of sand (particles > 63 microns) in 10 ml of sediment was about 10 g at stations 1 and 3 and 11 g at station 2. This amount, constituting about 95% of the sediment, varied little over the seasons and years.

MUD

The average weight of the mud or silt-clay fraction (particles < 63 microns) in 10 ml of sediment was about 0.4 g at station 1, 0.3 g at station 2 and 0.6 g at station 3. There was relatively little variation with years and seasons.

ORGANIC MATTER

The average weight of organic matter (material driven off by combustion) in 10 ml of sediment was about 0.3 g at stations 1 and 3 and 0.2 g at station 2. In 1992 and 1993, the average weight was about 0.3 g and in 1994–1996 about 0.2 g. In winter and spring the average weight was about 0.2 g while in summer and fall it was 0.3 g.

OXYGEN

Oxygen was measured in the years 1993–1996. At station 1 the average was about 6 mg/l, at station 2, 7 mg/l and at station 3, 5 mg/l. The average over all stations in 1993–1995 was about 6 mg/l; however, in 1996 it was 7 mg/l. During winter and spring, oxygen averaged about 7 mg/l, while in summer and fall about 6 mg/l. The minimum value recorded over the four year period was 2 mg/l in the summer of 1993 at station 2. These values indicate that each of the stations we occupied in the IRL was well oxygenated and well suited for aerobic organisms.

FORAMINIFERAL DENSITIES

We analyzed the observed densities of five foraminiferal taxa by constructing a general linear model (GLM) for each of the taxa. Each month from February, 1992 to February, 1997 four replicates were taken at each of three stations. We have, then, $12 \times 5 \times 4 \times 3 = 720 = n$ observations. The GLM for each taxon is constructed to test for hypotheses accounting for station differences (df = 2), years (df = 4), seasons (df = 3), station by years (df = 8), station by seasons (df = 6), years by seasons (df = 12), station by years by seasons (df = 24) and one or more environmental variables. Environmental variables were chosen for inclusion by examining foraminiferal density versus environmental variable(s) through step-wise regression, multiple regression and univariate regression. The GLM chosen for each taxon was one in which all hypotheses are significant.

QUINQUELOCULINA

This taxon, consisting of mostly *Q. impressa* and *Q. seminula,* averages about 120 individuals per 5 ml of sediment and makes up about 67% of the total number of living individuals. Multiple regression and step-wise regression identified temperature, salinity and mud as significant environmental variables. These variables along with vectors for testing station differences, yearly differences, seasonal differences and their interactions made up the initial GLM model. However, only temperature and mud proved significant in the final GLM model. Consequently, salinity was deleted. Table 1 shows the results of the GLM analysis in the standard ANOVA format. Although all the hypotheses for station, years, seasons and their interactions are significant, the sum-of-squares (SS) and mean-square (MS) for station differences are by far the largest. Station differences account for 0.35 of the R^2 of 0.62 or about 56% of the variance explained by the model. The large SS value for seasonal differences compared to years indicates more variation with seasons. The interaction hypotheses all have

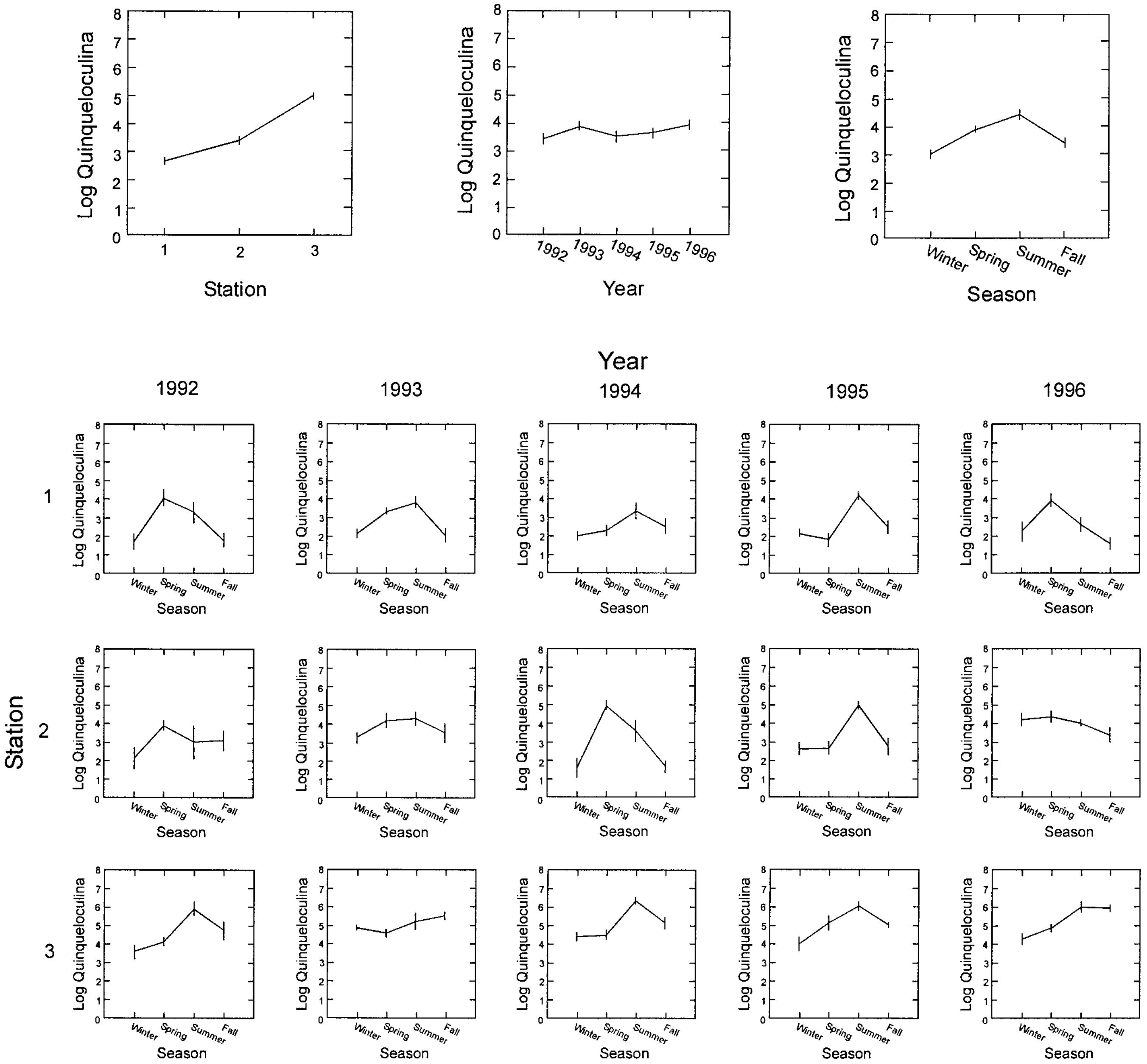

FIGURE 1. Mean ($\log_e$) densities for *Quinqueloculina* by station, year, season and their interactions.

large values of SS and collectively account for 0.14 of R^2 or about 23% of the explained variance. The environmental variables (temperature and mud), while significant, account for only 0.006 of R^2 or slightly less than 1% of the explained variance. In Figure 1 we show the mean densities for the four seasons broken down by years and stations. Although the densities usually increase from stations 1 to 3, as might be expected from the significance of the interaction hypotheses, the years and seasons vary at the stations. For example, while spring and summer are usually times of maximum density, during 1995 only summer showed a maximum.

ELPHIDIUM

This taxon, consisting mostly of *E. mexicanum* and *E. gunteri*, has an average density of 20 individuals per 5 ml of sediment, which comprises about 11% of the total number of living individuals. Multiple regression and step-wise regression identified temperature and salinity as significant variables. However, these variables were not significant when entered into the GLM. Consequently, Table 2 is a standard 3 way ANOVA table with all hypotheses statistically significant. Once again, the SS for stations is far larger than the rest and accounts for 0.14 of the 0.40 R^2 value or 35% of the explained variance. Figure 2 shows the mean densities at stations increase greatly from station 1 to 3 while differences are smaller among years and seasons. The significance of all the interaction hypotheses is evident from Figure 2, which indicates little synchrony. Although Spring and Summer are often times of maximum density, the maxima are not as pronounced for *Elphidium*, and there are more exceptions than for *Quinqueloculina*.

TABLE 2. General linear model for *Elphidium*.*

Source	Sum of squares	df	Mean square	F ratio	P
Stations	147.95	2	73.98	77.53	0.00
Years	26.89	4	6.72	7.05	0.00
Seasons	48.87	3	16.29	17.07	0.00
Stations × years	28.48	8	3.56	3.73	0.00
Stations × seasons	38.00	6	6.33	6.64	0.00
Years × seasons	47.03	12	3.92	4.11	0.00
Stations × years × seasons	82.38	24	3.43	3.60	0.00
Error	629.71	660	0.95		

* N = 720, R^2 = 0.40.

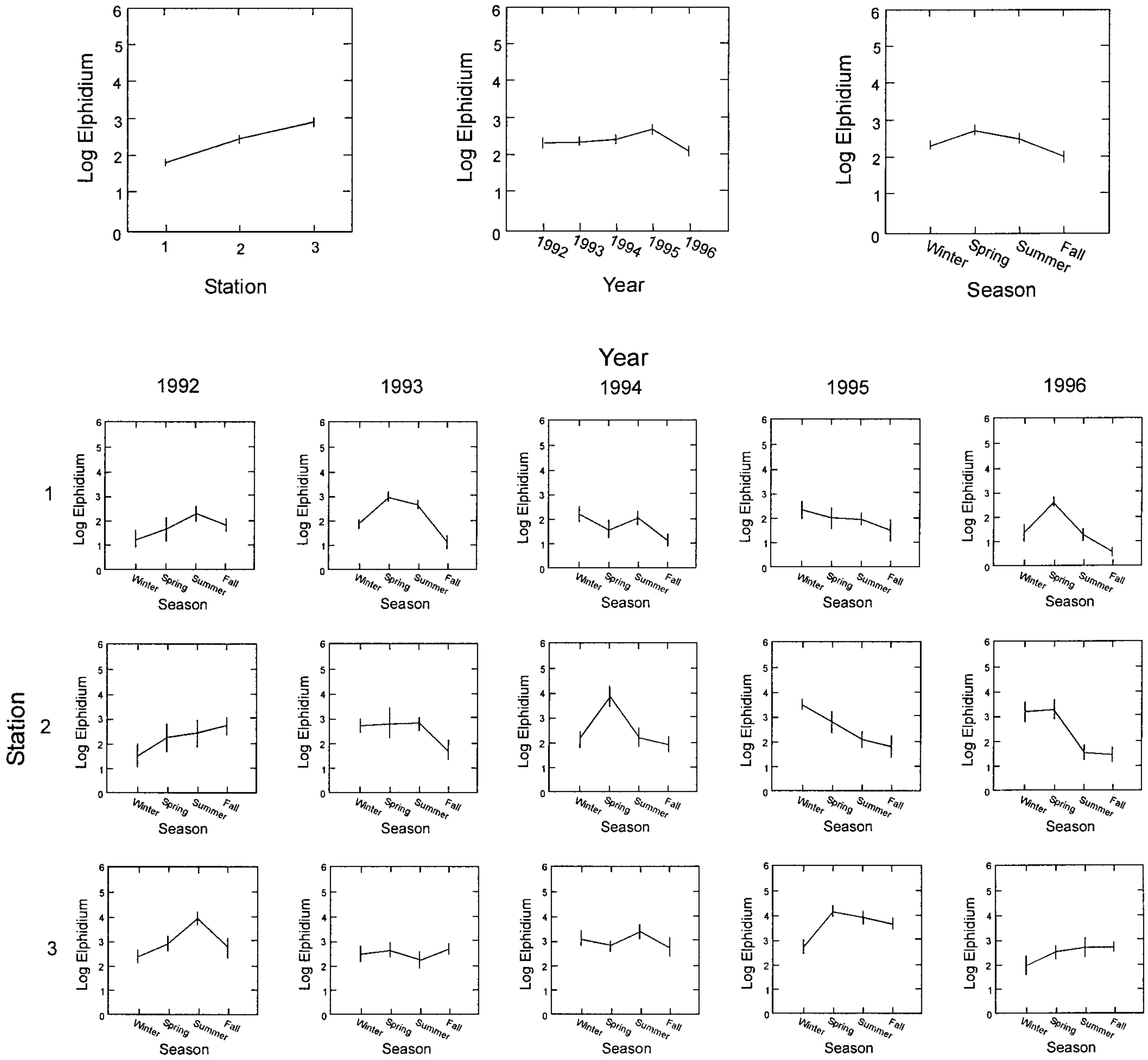

FIGURE 2. Mean ($\log_e$) densities for *Elphidium* by station, year, season and their interactions.

TABLE 3. General linear model for *Ammonia.**

Source	Sum of squares	df	Mean square	F ratio	P
Stations	335.58	2	167.79	193.92	0.00
Years	6.10	4	1.52	1.76	0.14
Seasons	14.23	3	4.74	5.48	0.00
Stations × years	58.14	8	7.27	8.40	0.00
Years × seasons	38.88	12	3.24	3.74	0.00
Stations × years × seasons	68.62	24	2.86	3.30	0.00
Error	576.25	666	0.86		

* N = 720, $R^2 = 0.48$.

AMMONIA

This taxon consists only of *A. beccarii* and has a mean density of about 26 individuals per 5 ml of sediment, which makes up about 15% of the total number of living individuals. Multiple regression and step-wise regression identified temperature, salinity and mud as significant environmental variables. However, the R^2 for all three together was only 0.07. In the original GLM model, none were significant. In addition, the hypotheses for years and station by seasons are not significant. In the GLM model we present here years is included because, although the hypothesis test for a years effect was not significant, the interaction hypotheses containing years are significant. Table 3 shows that, once again, the SS, MS and F-ratio for station differences are by far the largest, accounting for 0.31 of R^2 value of 0.48. This is about 65% of the explained variance. Looking at Figure 3, it is apparent why the interaction of stations by years by seasons is significant, but the lack of significance of the hypothesis for stations by seasons is not so easily understood. Fig. 4 shows that the three stations behave in the same manner with seasons and, at the same time, illustrates the importance of making field observations with a full factorial experimental design so that all combinations can be analyzed.

BOLIVINA

This taxon consists mainly of *B. striatula,* averages about 3 individuals per 5 ml, and comprises about 1% of the total. Multiple regression and step-wise regression identified sand, mud, and organic matter as significant environmental variables. The R^2 for all three is, however, only 0.03. In the initial GLM model none of these variables are significant and so all are excluded. Table 4 shows that all of the hypotheses tests for the 3-way ANOVA are significant. Once again the SS, MS and the F-ratio for the hypothesis station differences is the largest, accounting for 0.39 of the 0.57 value of R^2 or about 68% of the explained variance. Unlike the other taxa, however, the highest mean density for *Bolivina* is at station 1 instead of station 3 (Fig. 5). Spring and/or Summer were often times of density maxima and 1994 had low densities (Fig. 5).

AMMOBACULITES

This taxon is *A. exiguus* and averages about 9 individuals per 5 ml of sediment, which comprises 5% of the total. Analysis of species densities and environmental variables by multiple regression and step-wise regression indicated that salinity, pH and mud were significant variables. When these were included in a GLM, however, all were non-significant. All of the hypotheses for the three-way ANOVA were significant (Table 5). As with the other taxa, the SS, MS and the F-ratio for station differences are by far the largest contributor, comprising 0.29 of the 0.54 value of R^2 or about 54% of the explained variance. The increase in density from station 1 to 3 as with all the other taxa except for *Bolivina* is also observed (Fig. 6). The highest yearly density was in 1995 and this was mostly at station 3 (Fig. 6). Seasonally, spring and summer were often times of density maxima.

CORRELATION AMONG TAXA

The foregoing analyses indicate great similarity in the response of these taxa to the hypotheses tested. Figs. 1 through 5 indicate that, except for *Bolivina,* taxa exhibit an increase in density from station 1 to 3 and usually show spring and summer maxima. The results of the correlations between taxa as shown in Table 6 confirm the similarity. A high positive correlation exists between all pairs of taxa except for *Bolivina.* In the GLM analyses, environmental variables were significant only for *Quinqueloculina.* And, in this case, temperature and mud amounted to only 0.007 of the 0.62 value of R^2 (about 1%). The multiple regression on *Quinqueloculina* and temperature, salinity and mud, while significant, gave an R^2 of only 0.15. Moreover, regressions of significant environmental variables on the other taxa gave even lower values. Consequently, when treated as covariates in a GLM, the environmental variables contribute little to ‘‘explaining’’ the variability of observed densities. However, given the large correlations between taxa, the addition to the GLM of taxa as covariates ought to present a different picture. We will now proceed to examine this effect.

QUINQUELOCULINA

Table 6 indicates that the highest correlation with *Quinqueloculina* is *Ammonia.* Table 7 shows the GLM using *Ammonia.* Whereas station differences dominated the original GLM analysis (Table 1), the largest SS, MS and F-ratio by far is now due to *Ammonia.* The other hypotheses are still significant and the value of R^2 has increased from 0.62 to 0.78 with *Ammonia* accounting for about 60% of the explained variance. This is a substantial (26%) increase and is further illustrated by the observation that a multiple regression of *Quinqueloculina* versus temperature, salinity, and mud yields an R^2 of only 0.15 while a simple regression of *Quinqueloculina* versus *Ammonia* results in 0.47 (0.688^2,

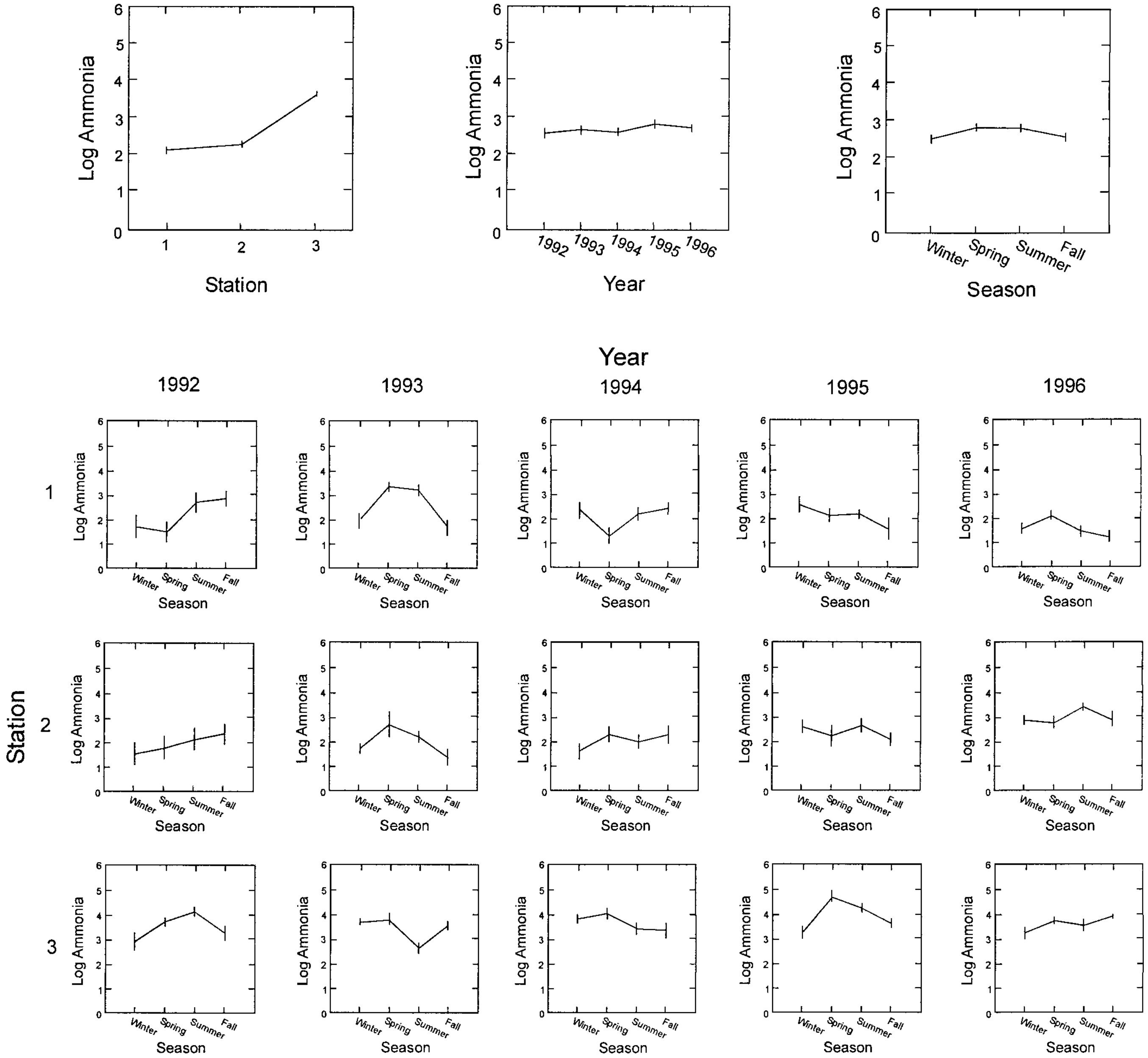

FIGURE 3. Mean ($\log_e$) densities for *Ammonia* by station, year, season and their interactions.

Table 6). A one-way ANOVA with stations yields a value of R^2 of 0.35. Thus, the best single predictor of *Quinqueloculina*'s density is another foraminiferal species.

ELPHIDIUM

Ammonia also has the highest correlation with *Elphidium* (Table 6). The GLM that includes *Ammonia* as a covariate is shown in Table 8. As in our previous analysis, the largest value of SS, MS and the F-ratio is now for *Ammonia;* the value of R^2 has increased 85% from 0.40 to 0.74, and *Ammonia* accounts for about 69% of the explained variance. A multiple regression with the significant environmental variables, temperature and salinity, gives an R^2 of only 0.02 and an ANOVA on stations gives a value of 0.14. A simple regression of *Elphidium* versus *Ammonia* gives an R^2 of 0.51, considerably higher than that for the entire GLM shown in Table 2.

AMMONIA

The GLM with *Elphidium* as a covariate is shown in Table 9. Once again, the covariate has the largest values of SS, MS and the F-ratio. A notable difference in this GLM (Table 9) is that the hypotheses for years and for seasons by stations now becomes significant when compared to the model shown in Table 3. The value of R^2 increases 60% from 0.48 to 0.77. A multiple regression with the significant environmental variables, temperature, salinity and mud, gives an $R^2 = 0.07$ and an R for ANOVA for stations of 0.31. The value of R^2 for a simple regression with *Elphi-*

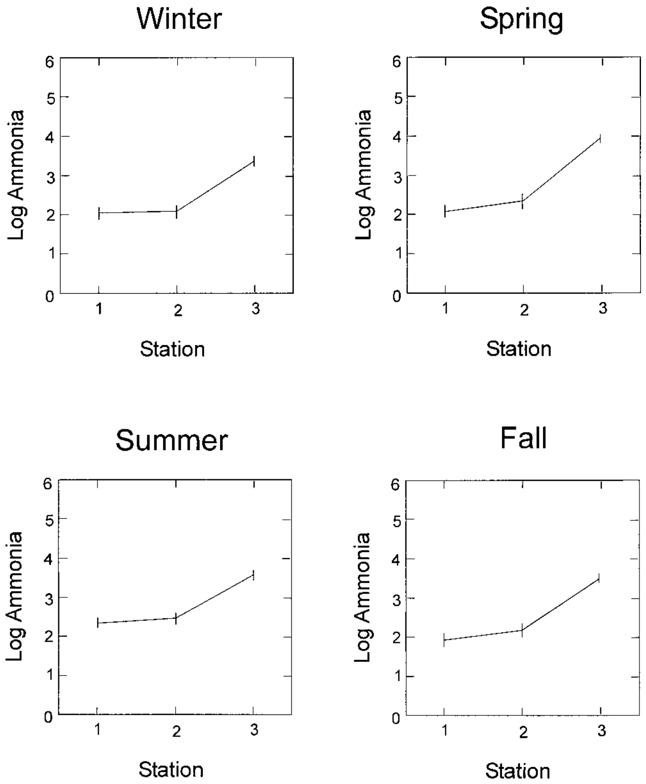

FIGURE 4. Mean ($\log_e$) densities for *Ammonia* for station by season.

dium is, as before, 0.51, slightly higher (6%) than the 0.48 for the GLM shown in Table 3.

BOLIVINA

As Table 6 indicates, *Bolivina* is the exception in that it does not correlate highly with the other taxa. Consequently, using *Ammonia* as a covariate increases R^2 only from 0.57 to 0.65 and the hypothesis for station differences still has the highest values for SS, MS and the F-ratio (Table 10). A multiple regression with sand, mud and organic matter as significant variables gave an R^2 of 0.02. An ANOVA for station differences yields an R^2 of 0.38 while a simple regression of *Bolivina* versus *Ammonia* yields an R^2 of 0.01.

AMMOBACULITES

Table 6 shows that *Ammobaculites* has the largest correlation with *Elphidium.* The GLM shown in Table 11 indicates that the largest SS, MS and F-ratio is now associated with this covariate. Also note that the hypothesis for years is now not significant, but remains in the model because the interactions with years are significant. The value of R^2 increases about 30% from 0.54 (Table 5) to 0.70 (Table 11). A multiple regression of the significant environmental variables of salinity, pH and mud yields an R^2 of 0.11 and an ANOVA on stations 0.29. A simple regression of *Ammobaculites* versus *Elphidium* gives an R^2 of 0.45.

LONG-TERM TREND

While the analyses above indicate significant differences among years for the taxa, they do not address a hypothesis of a long-term trend of increase or decrease in density during the five years of observations. To test this hypothesis, we calculated linear regressions for each taxa versus time (60 sampling times). For each of the five taxa, there is no significant result on the regression ANOVA and the R^2 in each case is 0.00. We have, then, no significant increase or decrease in the density of the taxa during the five years of observation. If the taxa are grouped by years, the results are also not significant. Consequently, despite all of the variability there is no overall increase or decrease in density.

DISCUSSION

Early studies of the life cycle and the seasonal distribution of *Elphidium crispum* indicated an alternation of generations and a simple cycle: reproduction occurred once a year in concert with the spring phytoplankton bloom and maximum densities could be observed at this time (Myers, 1942, 1943). The elegant simplicity of these observations encouraged field studies to examine living populations for similar patterns. For some species in some localities, a simple seasonal cycle is observed. For example, the reproductive cycle of *Glabratella ornatissima* produces high densities in spring and summer (Erskian and Lipps, 1987). However, laboratory and field studies of some common species indicate that this simple pattern is not usual and we would agree with Murray (1983) that “It is perhaps unfortunate that the early studies of the life cycle were concerned with *Elphidium crispum* . . .”. Observations on densities (standing crop) and size frequency distributions indicate that continuous or nearly continuous reproduction throughout the year is commonplace (e.g. Bradshaw, 1957, 1961; Phleger and Lankford, 1957; Boltovskoy, 1964; Buzas, 1965; Brooks, 1967; Wefer, 1976; Murray, 1983).

Nevertheless, species densities do often exhibit maximum densities at some particular time of a year. For example, we observed maximum densities for *Ammonia beccarii* during

TABLE 4. General linear model for *Bolivina.**

Source	Sum of squares	df	Mean square	F ratio	P
Stations	221.56	2	110.78	293.20	0.00
Years	13.35	4	3.34	8.84	0.00
Seasons	8.25	3	2.75	7.28	0.00
Stations × years	16.14	8	2.02	5.34	0.00
Stations × seasons	19.24	6	3.21	8.48	0.00
Years × seasons	13.80	12	1.15	3.04	0.00
Stations × years × seasons	34.37	24	1.43	3.79	0.00
Error	249.36	660	0.38		

* $N = 720$, $R^2 = 0.57$.

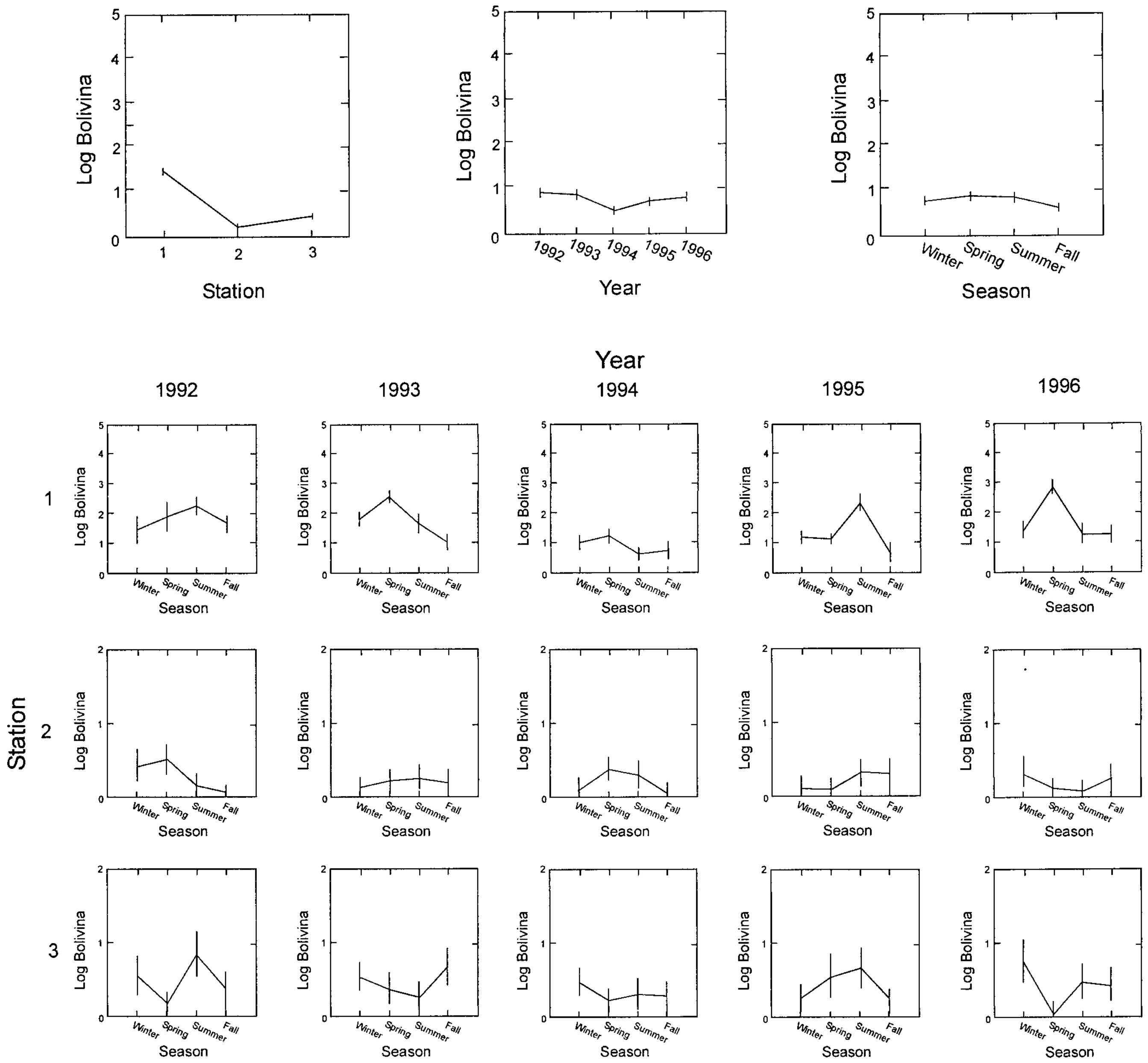

FIGURE 5. Mean ($\log_e$) densities for *Bolivina* by station, year, season and their interactions.

TABLE 5. General linear model for *Ammobaculites*.*

Source	Sum of squares	df	Mean square	F ratio	P
Stations	324.49	2	162.24	207.55	0.00
Years	20.24	4	5.06	6.47	0.00
Seasons	43.87	3	14.62	18.71	0.00
Stations × years	47.58	8	5.95	7.61	0.00
Stations × seasons	54.72	6	9.12	11.67	0.00
Years × seasons	41.43	12	3.45	4.42	0.00
Stations × years × seasons	75.36	24	3.14	4.02	0.00
Error	515.93	660	0.78		

* $N = 720$, $R^2 = 0.54$.

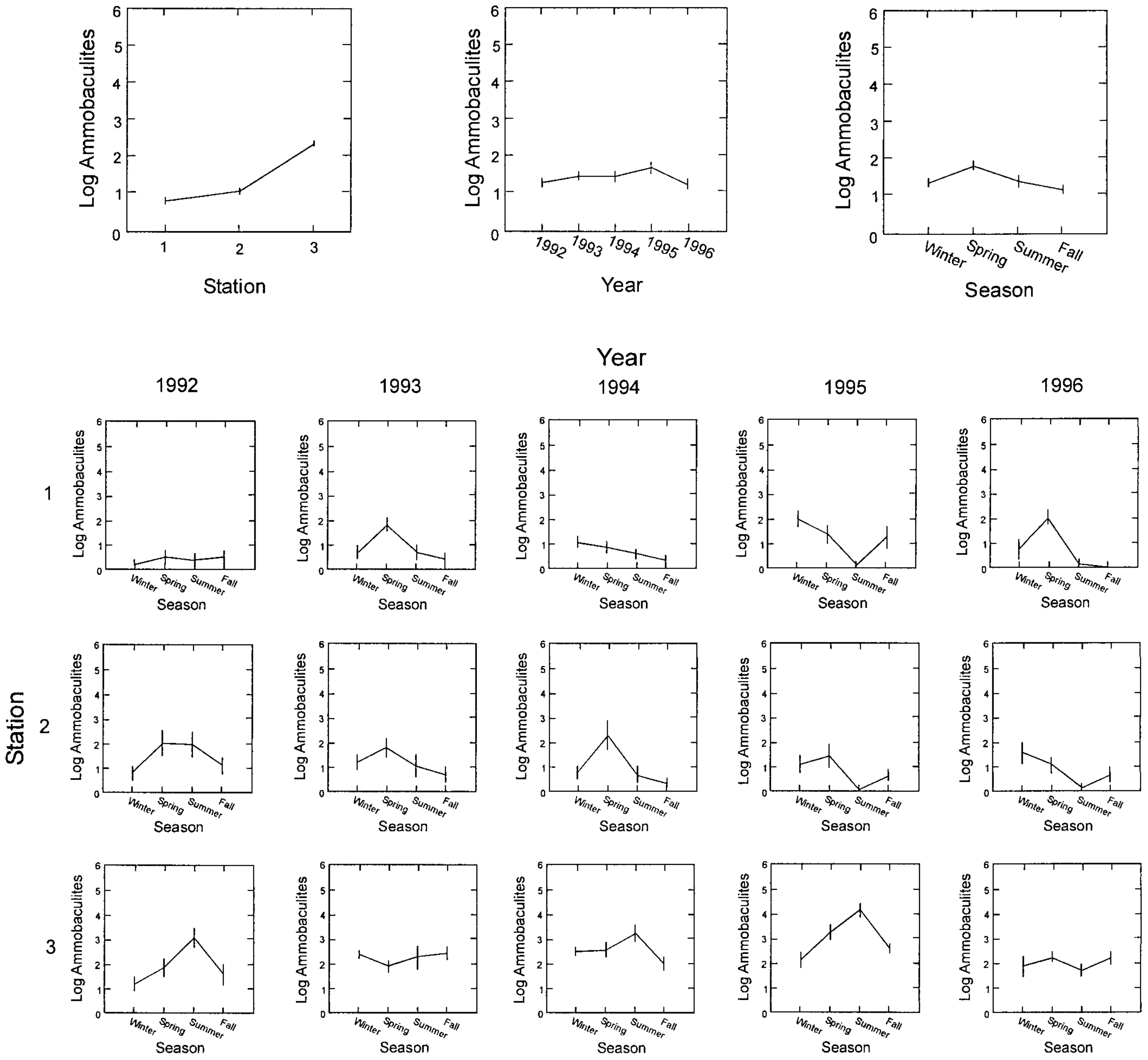

FIGURE 6. Mean ($\log_e$) densities for *Ammobaculites* by station, year, season and their interactions.

some summers as did Boltovskoy (1964) and Jones and Ross (1979). On the other hand, Murray and Alve (2000) observed a maximum for this species in fall and spring (as we sometimes did), while Boltovskoy and Lena (1969) observed a maximum in winter (as we sometimes did). To complete the ambiguity, Brooks (1967) in a very detailed study found no difference throughout the year for the same species.

As field observations extended beyond one year, the reason for some of these inconsistencies became obvious. Namely, foraminifera do not necessarily exhibit the same pattern and level of density from year to year (e.g. Lutze,

TABLE 6. Pearson correlation matrix.*

	log *Quinqueloculina*	log *Elphidium*	log *Ammonia*	log *Bolivina*	log *Ammobaculites*
log *Quinqueloculina*	1.000				
log *Elphidium*	0.635	1.000			
log *Ammonia*	0.688	0.712	1.000		
log *Bolivina*	0.031	0.068	0.100	1.000	
log *Ammobaculites*	0.608	0.669	0.616	−0.001	1.000

* N = 720.

TABLE 7. General linear model for *Quinqueloculina* with *Ammonia* as a covariate.*

Source	Sum of squares	df	Mean square	F ratio	P
Stations	115.24	2	57.62	88.45	0.00
Years	23.00	4	5.75	8.83	0.00
Seasons	114.67	3	38.22	58.68	0.00
Log *Ammonia*	318.76	1	318.76	489.31	0.00
Mud	4.12	1	4.12	6.32	0.01
Stations × years	23.13	8	2.89	4.44	0.00
Stations × seasons	74.17	6	12.36	18.98	0.00
Years × seasons	84.36	12	7.03	10.79	0.00
Stations × years × seasons	98.47	24	4.10	6.30	0.00
Error	428.65	658	0.65		

* $N = 720$, $R^2 = 0.78$

1968; Boltovskoy and Lena, 1969; Scott and Medioli, 1980; Basson and Murray, 1995; Murray and Alve, 2000; Buzas and Hayek, 2000). Although most of these studies did not extend beyond two and one-half years, the differences between years observed is substantiated by the 20 year observations presented by Buzas and Hayek (2000) and the current five year results.

The patchiness or aggregated distribution of foraminifera further complicates our observations (Buzas, 1968; Buzas, 1970). Although we do not show the results here, in the present study, we ran GLM's with replicates as a hypothesis. For each of the taxa there were no significant differences among replicates nor with the interactions of replicates by stations, years, and seasons. To illustrate the results we plot the outcome of a two-way ANOVA ($N = 720$) with *Quinqueloculina* as the dependent variable and stations and replicates as the independent variables (Fig. 7). As we might expect from examination of the plot, the difference among stations is significant, but the difference among replicates and their interaction by stations is not. Thus, in the IRL, the cores taken at each sampling time are replicates and we are confident that the observed changes in density are operating on a spatial scale of at least 1 m^2. While we would hope that observations at a single station are representative of a relatively large area (that is, >1 m^2) this may not be so.

Two studies have examined the spatial distribution of foraminifera in minute detail over a few cm^2 by constructing sampling devices with contiguous cells (Buzas, 1968; Olsson and Eriksson, 1974). In both studies, for most species the variance was greater than the mean and the appropriate probability distribution was the negative binomial rather than the Poisson. In the ecological literature, when the variance is $>$ mean, the terms ‘‘clumped’’ or more often ‘‘patchy’’ or ‘‘aggregated’’ are used interchangeably to describe the distribution. However, individuals, at this scale, are distributed in a continuum and clumps or patches are not discrete and can only arbitrarily be defined (Buzas and Gibson, 1990). Individuals are not distributed into discrete patches like stands of trees in a meadow, even though they are referred to as having a ‘‘patchy distribution’’. Obviously, sampling by contiguous cells cannot be carried out over an area much larger than a few cm^2. To overcome this difficulty, Buzas (1970) sampled a 4 × 4 grid of 16 stations each 10 m apart in Rehoboth Bay, Delaware. Each station was sampled with 5 replicates and homogeneity was defined as a lack of significant difference among stations. Notice that with this scheme we are no longer seeking to define a probability distribution in the usual way by examining the number of individuals per cell, but instead are doing so indirectly because for spatial distributions the variance is a function of the mean (for a thorough development of the topic see Hayek and Buzas, 1997, ch 6). In Rehoboth Bay, ANOVA's indicated that four of the five species enumerated had significant differences in density among the stations (inhomogeneous or heterogeneous). In 1970, laborious calculations carried out with a calculator during the analysis of the data indicated that only one station was different from the rest. Computer analysis of the same data, allowing for many contrasts to be performed easily, indicates four or five patches for *Ammonia* and *Elphidium* within the 1600 m^2. On a similar scale, Buzas and Severin (1993) sampled two stations in the IRL (one in sea-grass the other on bare sand), about 10 m apart, every fortnight for 10 months. Although the overall density between stations did not differ for most taxa, the periodicity at each was different. Consequently, had we sampled the area at a single time, the densities

TABLE 8. General linear model for *Elphidium* with *Ammonia* as a covariate.*

Source	Sum of squares	df	Mean square	F ratio	P
Stations	48.01	2	24.00	56.80	0.00
Years	22.18	4	5.54	13.12	0.00
Seasons	24.92	3	8.31	19.66	0.00
Log *Ammonia*	351.21	1	351.21	831.07	0.00
Stations × years	25.27	8	3.16	7.47	0.00
Stations × seasons	51.03	6	8.50	20.12	0.00
Years × seasons	29.13	12	2.43	5.74	0.00
Stations × years × seasons	40.32	24	1.68	3.98	0.00
Error	278.49	659	0.42		

* $N = 720$, $R^2 = 0.74$.

TABLE 9. General linear model for *Ammonia* with *Elphidium* as a covariate.*

Source	Sum of squares	df	Mean square	F ratio	P
Stations	128.18	2	64.09	168.27	0.00
Years	11.68	4	2.92	7.67	0.00
Seasons	9.13	3	3.04	7.99	0.00
Log *Elphidium*	316.53	1	316.53	831.07	0.00
Stations × years	37.76	8	4.72	12.39	0.00
Stations × seasons	33.40	6	5.57	14.61	0.00
Years × seasons	24.66	12	2.06	5.40	0.00
Stations × years × seasons	33.82	24	1.41	3.70	0.00
Error	250.99	659	0.38		

* $N = 720$, $R^2 = 0.77$

would have been significantly different. Similarly, Murray and Alve (2000) sampled two stations, one at 1.5 m and the other 2.2 m above chart datum, over a 27 month period and observed an annual cyclicity at one station, but not at the other. The differences in periodicity over a distance of a few meters might be attributed to differing habitats, for example, seagrass vs bare sand or the amount of exposure and so on, but we do not think so.

Based on the spatial observations cited above, we believe that another explanation is more likely and here propose a model of asynchronous or aperiodic pulsating patches. Spatial studies, typically done at a single sampling time, indicate spatial patchiness on a scale of a few meters within what may be judged as a single habitat (Buzas, 1970). If the foraminifera within each patch reproduce without synchrony, then we would observe not only differences in density with time at a patch, but also a change in the spatial position of patches with time. Over a scale of a few meters, we would observe asynchronous pulsating patches. An analogy can be visualized by considering the wall structure of an optically granular wall of a foraminifer under cross polarized light as seen in a petrographic microscope. What appears is a mosaic of grains with slightly different colors. As the stage is rotated various grains haphazardly go in and out of extinction. If we imagine the colors or lack of them as density and the rotation as time, we have a graphic concept of the principle. The microscope example is, however, synchronous by grain in that extinction always occurs with the same amount of rotation on a particular grain while in our model this need not necessarily be so.

In the present study, stations 1 and 2 are about 0.5 km apart and the analyses as well as the plots of Figs. 1, 2, 3, 5 and 6 show that the variability between stations is very large. Over a period of five years, hypotheses for station differences, yearly differences, seasonal differences and all their interactions are significant. In other words, the observed densities of the foraminifera are as complicated as possible. For a model advocating asynchronous pulsating patches, on the larger scale of the present study, we would also expect to find significant differences in densities among stations, years, seasons and their interactions, and we have.

Given the large differences in observed densities in only a few meters, it is not surprising that the commonly measured environmental variables, which are invariant on larger scales, explain very little of the overall observed variability. At the same time, the densities of four of the five taxa studied here are highly correlated; thus, the taxa may respond together to the same abiotic or biotic cue. Clearly, they are not competing with one another because the best predictor of species variation in density is the density (positive) of another foraminiferal species. Why this is so remains a mystery.

Although seasonal and yearly differences were large, Buzas and Hayek (2000) found no overall trend for increase or decrease in density in the IRL over a period of 20 years. Over the shorter 5 year time frame of this study, the 3 stations also did not exhibit any overall increase or decrease in density. Even though large amounts of spatial and temporal variability at stations only a few meters apart are observed, this does not necessarily imply long-term instability. Curiously, the large amount of variability in small amounts of space and time may be the foraminiferal strategy to insure long-term stability. And a population model of asynchronous pulsating patches describes this structural stability.

The spatial-temporal complexities demonstrated here might be viewed by some as negatively reflecting upon the use of foraminifera as faunal barometers for the health and stability of a lagoon or estuary. However, we do not think

TABLE 10. General linear model for *Bolivina* with *Ammonia* as a covariate.*

Source	Sum of squares	df	Mean square	F ratio	P
Stations	265.64	2	132.82	432.08	0.00
Years	14.21	4	3.55	11.56	0.00
Seasons	4.63	3	1.54	5.02	0.00
Log *Ammonia*	46.79	1	46.79	152.21	0.00
Stations × years	20.36	8	2.55	8.28	0.00
Stations × seasons	23.59	6	3.93	12.79	0.00
Years × seasons	11.72	12	0.98	3.18	0.00
Stations × years × seasons	28.73	24	1.20	3.89	0.00
Error	202.58	659	0.31		

* $N = 720$, $R^2 = 0.65$.

TABLE 11. General linear model for *Ammobaculites* with *Elphidium* as a covariate.*

Source	Sum of squares	df	Mean square	F ratio	P
Stations	140.11	2	70.06	138.18	0.00
Years	4.35	4	1.09	2.14	0.07
Seasons	11.03	3	3.68	7.25	0.00
Log *Elphidium*	181.83	1	181.83	358.66	0.00
Stations × years	44.87	8	5.61	11.06	0.00
Stations × seasons	34.43	6	5.74	11.32	0.00
Years × seasons	15.48	12	1.29	2.54	0.00
Stations × years × seasons	43.64	24	1.82	3.59	0.00
Error	334.10	659	0.51		

* $N = 720$, $R^2 = 0.70$.

so. Rather, the opposite is more likely true. Spatially, the small size of the foraminifera (say, 0.05 cm in size) compared to a macrofaunal organism (say, 5 cm in size) makes 10 meters for a foraminifer equivalent to 1 Km for the larger organisms. Temporally, the foraminifera with several generations per year allow us to chart changes in the density of many generations over a 5 year span. For larger organisms with one or a few generations per year the equivalent amount of information would require decades of observation. Indeed, we speculate that the idea of pulsating patches is relevant for benthic macrofaunal organisms, but long-term studies with suitable scaling and experimental design have not been done. While the results of this study clearly indicate that observations at a single station are not indicative of a much larger area at any particular time, the concept of pulsating patches indicates that observations on a particular patch or station will in the long-term give an assessment of a much larger area.

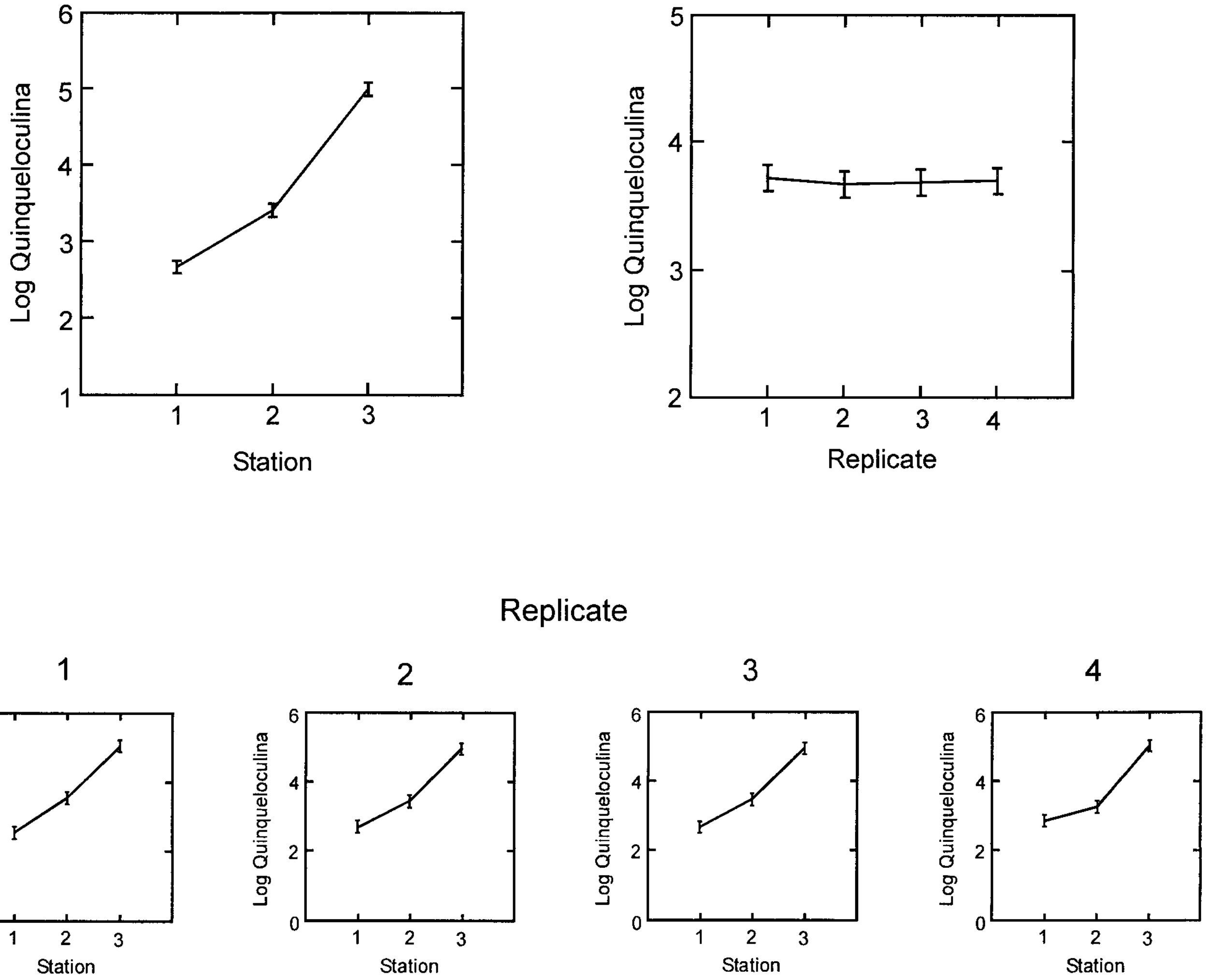

FIGURE 7. Mean ($\log_e$) densities for *Quinqueloculina* by station and replicate and their interaction.

ACKNOWLEDGMENTS

We thank Dr. Mary Rice and the staff at the Smithsonian Marine Station at Fort Pierce for their help. This is contribution number 522 from the Smithsonian Marine Station at Fort Pierce.

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Received 13 February 2001
Accepted 15 May 2001

APPENDIX. Counts of living (stained) foraminifera in 5 ml of sediment in the Indian River, Florida. Station 1: 27° 32.05′ N, 80° 20.8′ W. Station 2: 27° 31.8′ N, 80° 20.8′ W. Station 3: 27° 29.2′ N, 80° 18.2′ W. Water depth about 1 m. Year 1: February 1992–January 1993; . . . ; Year 5: February 1996–January 1997. Replicates: 1, 2, 3, 4 were taken within a few minutes of each other and within 1 m^2.

Station	Year	Month	Replicate	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*
1	1	Feb	1	0	0	0	0	0
1	1		2	3	0	0	0	0
1	1		3	0	0	0	0	0
1	1		4	1	0	0	0	0
1	1	Mar	1	8	0	0	0	0
1	1		2	10	0	0	0	0
1	1		3	62	0	0	0	0
1	1		4	4	0	0	0	0
1	1	Apr	1	133	15	20	19	2
1	1		2	262	38	20	36	2
1	1		3	70	10	8	7	2
1	1		4	349	66	40	40	5
1	1	May	1	104	5	5	14	0
1	1		2	65	3	2	14	1
1	1		3	99	6	5	11	0
1	1		4	96	6	4	11	0
1	1	Jun	1	25	8	3	13	0
1	1		2	15	3	6	6	0
1	1		3	110	23	31	16	2
1	1		4	56	14	9	8	0
1	1	Jul	1	2	2	2	5	0
1	1		2	77	23	72	30	2
1	1		3	5	2	11	7	0
1	1		4	20	8	8	6	0
1	1	Aug	1	51	8	32	4	0
1	1		2	4	7	6	1	0
1	1		3	6	7	10	5	1
1	1		4	938	56	230	65	4
1	1	Sep	1	23	11	82	17	0
1	1		2	6	14	28	3	1
1	1		3	9	14	45	3	0
1	1		4	4	7	9	3	0
1	1	Oct	1	8	9	27	5	2
1	1		2	4	1	14	3	3
1	1		3	25	6	41	10	3
1	1		4	23	12	29	14	3
1	1	Nov	1	1	4	8	6	0
1	1		2	2	3	7	2	0
1	1		3	0	0	2	1	0
1	1		4	1	2	5	1	0
1	1	Dec	1	13	10	23	8	0
1	1		2	1	2	5	1	0
1	1		3	3	4	20	1	0
1	1		4	14	15	51	15	0
1	1	Jan	1	5	1	2	7	1
1	1		2	23	4	15	16	0
1	1		3	13	9	9	14	0
1	1		4	44	9	12	36	2
1	2	Feb	1	15	6	3	19	0
1	2		2	22	12	14	9	1
1	2		3	1	3	8	1	0
1	2		4	8	5	3	8	0
1	2	Mar	1	21	7	16	9	3
1	2		2	29	14	24	16	8
1	2		3	33	14	20	15	8
1	2		4	20	15	10	16	1
1	2	Apr	1	35	9	33	9	10
1	2		2	47	25	39	15	13
1	2		3	11	14	16	10	4
1	2		4	10	11	21	6	5
1	2	May	1	27	30	40	6	1
1	2		2	47	44	42	14	5
1	2		3	36	20	35	13	21
1	2		4	45	43	61	32	11
1	2	Jun	1	117	25	47	8	10
1	2		2	66	24	58	11	4
1	2		3	58	22	59	19	4
1	2		4	48	23	42	4	2
1	2	Jul	1	29	5	9	3	0

APPENDIX. Continued.

Station	Year	Month	Replicate	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*
1	2		2	17	11	20	0	0
1	2		3	90	9	25	4	1
1	2		4	43	11	14	2	1
1	2	Aug	1	10	8	14	4	0
1	2		2	18	9	5	1	0
1	2		3	57	11	26	5	2
1	2		4	133	9	23	10	0
1	2	Sep	1	1	2	2	1	0
1	2		2	15	5	5	3	1
1	2		3	12	1	6	2	0
1	2		4	2	2	0	0	0
1	2	Oct	1	34	0	5	7	2
1	2		2	12	2	9	1	0
1	2		3	1	0	11	0	0
1	2		4	0	0	0	0	0
1	2	Nov	1	7	4	3	2	0
1	2		2	13	4	11	3	4
1	2		3	14	5	10	7	0
1	2		4	24	4	10	4	8
1	2	Dec	1	5	6	8	8	1
1	2		2	15	10	22	8	6
1	2		3	8	3	20	5	1
1	2		4	6	5	2	2	2
1	2	Jan	1	4	7	9	4	0
1	2		2	7	7	2	2	3
1	2		3	5	1	0	3	2
1	2		4	17	5	13	7	4
1	3	Feb	1	8	4	2	4	4
1	3		2	6	1	1	2	2
1	3		3	7	9	6	2	7
1	3		4	14	7	3	3	3
1	3	Mar	1	17	26	5	8	8
1	3		2	5	13	8	3	3
1	3		3	16	15	8	3	6
1	3		4	5	7	2	5	0
1	3	Apr	1	3	2	10	7	0
1	3		2	1	3	6	2	1
1	3		3	8	6	9	2	1
1	3		4	8	4	3	3	2
1	3	May	1	18	1	0	3	1
1	3		2	15	1	0	2	0
1	3		3	10	1	1	0	1
1	3		4	32	0	0	0	2
1	3	Jun	1	21	3	7	2	3
1	3		2	29	10	14	1	1
1	3		3	9	5	3	0	0
1	3		4	11	6	14	3	1
1	3	Jul	1	6	4	8	1	1
1	3		2	14	5	7	4	2
1	3		3	9	3	6	1	1
1	3		4	14	2	4	0	0
1	3	Aug	1	275	30	49	1	1
1	3		2	104	12	5	1	0
1	3		3	201	25	28	0	2
1	3		4	37	3	1	0	1
1	3	Sep	1	2	0	2	0	0
1	3		2	11	2	6	2	1
1	3		3	47	5	18	8	0
1	3		4	6	3	18	3	0
1	3	Oct	1	3	3	6	0	0
1	3		2	4	2	4	1	0
1	3		3	12	3	11	0	2
1	3		4	11	0	5	0	0
1	3	Nov	1	2	2	12	0	0
1	3		2	32	2	17	1	1
1	3		3	54	3	20	4	1
1	3		4	55	4	44	3	3
1	3	Dec	1	2	5	10	0	2
1	3		2	3	6	13	1	1
1	3		3	10	8	15	2	2
1	3		4	8	4	10	0	0
1	3	Jan	1	7	6	14	4	3

APPENDIX. Continued.

Station	Year	Month	Replicate	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*
1	3		2	23	49	54	6	3
1	3		3	2	14	21	2	1
1	3		4	7	30	27	1	1
1	4	Feb	1	6	11	25	2	3
1	4		2	12	41	49	8	15
1	4		3	12	31	30	6	12
1	4		4	14	36	54	2	15
1	4	Mar	1	15	7	19	4	7
1	4		2	2	6	10	1	1
1	4		3	8	5	16	2	7
1	4		4	0	6	2	2	3
1	4	Apr	1	3	60	1	1	0
1	4		2	20	32	20	2	11
1	4		3	19	38	22	3	19
1	4		4	20	17	9	4	4
1	4	May	1	0	1	3	0	0
1	4		2	6	0	2	2	0
1	4		3	2	6	7	3	3
1	4		4	7	21	10	4	5
1	4	Jun	1	48	15	25	12	0
1	4		2	53	16	8	4	0
1	4		3	99	1	3	9	0
1	4		4	57	5	12	4	1
1	4	Jul	1	34	5	2	4	0
1	4		2	62	4	10	3	0
1	4		3	43	5	8	14	0
1	4		4	45	10	5	5	0
1	4	Aug	1	141	7	9	42	1
1	4		2	104	6	9	25	0
1	4		3	107	8	9	19	0
1	4		4	63	3	9	13	0
1	4	Sep	1	13	0	0	0	2
1	4		2	26	4	14	9	5
1	4		3	6	0	0	0	0
1	4		4	7	0	0	0	2
1	4	Oct	1	14	15	23	3	17
1	4		2	21	14	34	9	43
1	4		3	14	5	6	0	7
1	4		4	13	5	15	2	7
1	4	Nov	1	0	0	0	0	0
1	4		2	5	1	0	0	0
1	4		3	21	23	16	0	0
1	4		4	29	19	4	1	1
1	4	Dec	1	6	7	14	2	7
1	4		2	10	18	22	6	25
1	4		3	3	11	8	2	16
1	4		4	6	9	11	3	7
1	4	Jan	1	7	1	3	0	1
1	4		2	16	9	7	1	2
1	4		3	5	2	3	2	5
1	4		4	5	1	1	1	1
1	5	Feb	1	61	11	5	3	12
1	5		2	58	11	8	6	8
1	5		3	28	8	7	4	8
1	5		4	51	14	9	3	6
1	5	Mar	1	122	10	21	43	22
1	5		2	75	9	5	12	8
1	5		3	63	9	8	20	7
1	5		4	94	9	19	30	8
1	5	Apr	1	29	9	3	13	3
1	5		2	126	24	7	31	19
1	5		3	72	19	9	8	17
1	5		4	121	28	11	24	12
1	5	May	1	13	16	9	16	1
1	5		2	19	6	2	11	2
1	5		3	8	6	2	4	2
1	5		4	44	27	8	28	12
1	5	Jun	1	3	6	2	5	0
1	5		2	5	3	3	4	0
1	5		3	2	1	1	0	0
1	5		4	9	11	11	23	2

APPENDIX. Continued.

Station	Year	Month	Replicate	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*
1	5	Jul	1	8	2	1	3	0
1	5		2	6	0	2	1	0
1	5		3	34	1	1	1	0
1	5		4	23	1	2	0	0
1	5	Aug	1	73	5	14	14	0
1	5		2	18	5	3	1	0
1	5		3	18	1	4	2	0
1	5		4	34	4	9	5	2
1	5	Sep	1	4	1	7	7	0
1	5		2	2	2	2	1	0
1	5		3	5	1	5	5	0
1	5		4	6	1	6	8	0
1	5	Oct	1	17	4	10	8	0
1	5		2	3	1	3	5	0
1	5		3	5	1	4	3	0
1	5		4	12	1	2	4	0
1	5	Nov	1	9	0	0	2	0
1	5		2	1	0	1	0	0
1	5		3	1	0	1	1	0
1	5		4	0	0	0	0	0
1	5	Dec	1	20	5	5	2	0
1	5		2	1	1	2	0	0
1	5		3	5	1	4	3	0
1	5		4	27	1	4	12	0
1	5	Jan	1	1	1	0	5	0
1	5		2	0	0	2	0	0
1	5		3	2	1	5	9	0
1	5		4	1	1	3	3	0
2	1	Feb	1	0	0	0	0	0
2	1		2	0	0	0	0	0
2	1		3	0	0	0	0	0
2	1		4	2	0	0	0	1
2	1	Mar	1	24	0	0	0	0
2	1		2	24	0	0	0	1
2	1		3	11	0	0	0	0
2	1		4	36	0	0	0	2
2	1	Apr	1	67	22	6	1	3
2	1		2	64	41	11	1	4
2	1		3	74	41	12	5	8
2	1		4	19	6	2	1	3
2	1	May	1	91	34	28	1	34
2	1		2	79	29	21	0	81
2	1		3	113	38	30	2	49
2	1		4	129	52	27	1	51
2	1	Jun	1	0	2	2	0	0
2	1		2	6	12	4	0	2
2	1		3	129	34	14	2	3
2	1		4	139	20	8	1	2
2	1	Jul	1	1	5	2	0	5
2	1		2	0	0	1	0	6
2	1		3	0	1	1	0	4
2	1		4	0	0	0	0	0
2	1	Aug	1	1061	117	105	0	118
2	1		2	524	49	31	0	45
2	1		3	42	25	16	0	16
2	1		4	574	79	82	0	27
2	1	Sep	1	15	29	11	0	0
2	1		2	77	27	29	0	4
2	1		3	25	19	16	0	5
2	1		4	8	25	11	0	3
2	1	Oct	1	66	7	13	0	1
2	1		2	647	65	141	1	22
2	1		3	30	21	8	0	0
2	1		4	99	27	12	0	8
2	1	Nov	1	3	19	8	0	3
2	1		2	4	7	0	0	3
2	1		3	7	1	10	0	0
2	1		4	1	2	0	0	0
2	1	Dec	1	63	33	27	4	4
2	1		2	32	14	20	3	4
2	1		3	36	7	6	3	0
2	1		4	0	0	0	0	0

APPENDIX. Continued.

Station	Year	Month	Replicate	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*
2	1	Jan	1	59	14	20	0	5
2	1		2	83	26	23	0	4
2	1		3	12	6	5	1	1
2	1		4	10	7	9	0	3
2	2	Feb	1	18	4	10	0	0
2	2		2	9	4	1	0	1
2	2		3	6	5	5	0	1
2	2		4	6	7	1	0	0
2	2	Mar	1	5	0	0	0	0
2	2		2	15	0	0	0	0
2	2		3	158	15	12	0	13
2	2		4	18	0	0	0	0
2	2	Apr	1	123	50	35	2	16
2	2		2	79	37	27	0	6
2	2		3	153	35	52	0	17
2	2		4	130	20	26	1	7
2	2	May	1	139	126	69	0	5
2	2		2	58	54	39	1	5
2	2		3	52	31	25	0	14
2	2		4	165	70	88	0	13
2	2	Jun	1	97	16	11	0	0
2	2		2	28	28	3	0	0
2	2		3	55	31	4	0	1
2	2		4	100	30	15	1	0
2	2	Jul	1	208	38	24	1	26
2	2		2	235	30	20	1	37
2	2		3	62	13	13	1	8
2	2		4	7	8	3	0	0
2	2	Aug	1	164	10	6	1	1
2	2		2	23	3	4	0	0
2	2		3	46	8	4	0	0
2	2		4	243	14	16	0	6
2	2	Sep	1	31	9	4	0	0
2	2		2	24	9	3	0	0
2	2		3	51	12	5	1	2
2	2		4	31	5	7	1	1
2	2	Oct	1	570	28	28	1	13
2	2		2	128	5	5	0	4
2	2		3	169	14	9	1	3
2	2		4	59	10	3	0	1
2	2	Nov	1	1	0	0	0	0
2	2		2	10	1	0	0	0
2	2		3	12	0	0	0	0
2	2		4	3	0	1	0	0
2	2	Dec	1	27	17	7	0	2
2	2		2	32	29	2	0	3
2	2		3	61	25	7	0	1
2	2		4	132	24	10	0	3
2	2	Jan	1	54	27	6	3	19
2	2		2	20	9	5	0	2
2	2		3	47	35	7	0	13
2	2		4	18	18	4	0	4
2	3	Feb	1	40	40	10	1	5
2	3		2	30	4	0	0	0
2	3		3	67	31	6	0	2
2	3		4	17	6	0	0	2
2	3	Mar	1	199	258	26	1	149
2	3		2	173	122	17	0	88
2	3		3	120	222	14	1	129
2	3		4	24	82	7	0	4
2	3	Apr	1	154	26	13	0	1
2	3		2	237	105	40	1	6
2	3		3	187	15	14	0	3
2	3		4	120	59	16	0	4
2	3	May	1	96	5	1	2	3
2	3		2	195	11	1	1	26
2	3		3	189	40	8	1	0
2	3		4	232	39	2	0	3
2	3	Jun	1	340	55	46	0	10
2	3		2	34	17	6	0	0
2	3		3	31	9	8	0	1

APPENDIX. Continued.

Station	Year	Month	Replicate	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*
2	3		4	188	42	34	0	8
2	3	Jul	1	68	14	6	1	1
2	3		2	358	15	12	0	5
2	3		3	54	1	2	0	1
2	3		4	61	8	2	0	0
2	3	Aug	1	0	3	2	0	0
2	3		2	6	2	2	1	0
2	3		3	19	5	3	2	0
2	3		4	7	2	8	2	0
2	3	Sep	1	0	1	1	0	0
2	3		2	2	4	2	0	0
2	3		3	4	1	1	0	0
2	3		4	2	3	7	0	0
2	3	Oct	1	6	17	36	0	0
2	3		2	0	2	2	0	0
2	3		3	13	8	12	0	1
2	3		4	11	16	30	0	4
2	3	Nov	1	5	14	14	0	0
2	3		2	8	7	9	0	2
2	3		3	15	18	61	0	0
2	3		4	7	10	14	0	1
2	3	Dec	1	0	9	10	0	1
2	3		2	1	8	7	0	0
2	3		3	2	5	10	0	1
2	3		4	0	0	1	0	0
2	3	Jan	1	4	10	6	0	4
2	3		2	0	5	8	0	1
2	3		3	4	11	8	1	3
2	3		4	0	6	2	0	0
2	4	Feb	1	9	29	42	0	6
2	4		2	12	46	20	1	3
2	4		3	2	11	8	0	0
2	4		4	1	16	25	0	2
2	4	Mar	1	47	44	27	0	30
2	4		2	11	17	15	0	14
2	4		3	26	29	11	0	15
2	4		4	2	1	1	0	1
2	4	Apr	1	60	106	91	0	13
2	4		2	7	18	9	0	0
2	4		3	12	29	17	0	13
2	4		4	41	92	24	0	13
2	4	May	1	18	23	19	2	0
2	4		2	4	1	1	0	0
2	4		3	8	7	1	0	0
2	4		4	7	3	0	0	0
2	4	Jun	1	462	40	130	1	0
2	4		2	203	20	35	0	1
2	4		3	152	9	22	0	0
2	4		4	105	9	19	0	0
2	4	Jul	1	309	0	5	0	0
2	4		2	160	4	12	1	0
2	4		3	73	5	9	0	1
2	4		4	56	3	4	0	0
2	4	Aug	1	133	7	5	1	0
2	4		2	112	6	6	1	0
2	4		3	136	10	18	1	0
2	4		4	129	15	8	1	0
2	4	Sep	1	29	12	11	1	0
2	4		2	46	6	9	0	0
2	4		3	29	6	8	0	4
2	4		4	98	5	17	0	1
2	4	Oct	1	26	30	13	0	2
2	4		2	18	59	26	0	3
2	4		3	18	12	5	0	3
2	4		4	32	8	18	0	1
2	4	Nov	1	5	1	2	2	0
2	4		2	2	0	2	1	1
2	4		3	7	1	3	2	1
2	4		4	0	0	1	1	0
2	4	Dec	1	35	102	41	0	6
2	4		2	35	100	22	0	14
2	4		3	13	46	15	0	10

APPENDIX. Continued.

Station	Year	Month	Replicate	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*
2	4		4	7	35	11	1	3
2	4	Jan	1	33	20	5	0	0
2	4		2	29	21	2	0	0
2	4		3	22	27	4	0	1
2	4		4	22	33	8	0	0
2	5	Feb	1	163	148	22	0	15
2	5		2	128	100	16	0	26
2	5		3	18	27	8	0	11
2	5		4	101	61	25	0	36
2	5	Mar	1	180	93	27	0	3
2	5		2	139	97	12	1	7
2	5		3	22	23	3	0	2
2	5		4	255	130	31	1	15
2	5	Apr	1	64	29	22	0	1
2	5		2	30	23	11	0	1
2	5		3	48	32	11	0	6
2	5		4	51	36	6	0	1
2	5	May	1	44	1	5	0	0
2	5		2	207	26	52	0	1
2	5		3	50	5	32	0	0
2	5		4	165	15	13	0	1
2	5	Jun	1	48	12	41	0	0
2	5		2	66	11	15	0	0
2	5		3	75	12	25	1	0
2	5		4	45	10	25	0	0
2	5	Jul	1	119	4	48	0	0
2	5		2	64	1	18	0	0
2	5		3	46	1	20	0	0
2	5		4	79	1	17	0	0
2	5	Aug	1	27	5	30	0	0
2	5		2	38	1	29	0	2
2	5		3	52	3	77	0	1
2	5		4	43	2	31	0	0
2	5	Sep	1	151	14	84	0	1
2	5		2	103	6	42	1	0
2	5		3	153	7	79	2	0
2	5		4	39	2	16	1	0
2	5	Oct	1	42	8	31	0	2
2	5		2	25	0	12	0	0
2	5		3	11	1	14	0	0
2	5		4	13	3	10	0	0
2	5	Nov	1	3	0	2	0	1
2	5		2	6	3	5	0	6
2	5		3	38	6	10	1	8
2	5		4	19	6	12	0	3
2	5	Dec	1	77	13	35	1	6
2	5		2	105	19	36	0	0
2	5		3	53	10	13	1	2
2	5		4	29	4	6	0	2
2	5	Jan	1	112	26	19	5	2
2	5		2	10	3	7	0	1
2	5		3	214	58	33	1	0
2	5		4	49	14	10	0	1
3	1	Feb	1	35	12	6	0	3
3	1		2	48	29	36	0	2
3	1		3	42	16	16	1	9
3	1		4	1	3	0	0	1
3	1	Mar	1	22	6	10	0	8
3	1		2	40	8	33	0	1
3	1		3	76	13	25	0	13
3	1		4	59	29	34	1	15
3	1	Apr	1	57	19	65	1	14
3	1		2	15	14	24	0	2
3	1		3	104	71	30	2	26
3	1		4	72	123	83	0	2
3	1	May	1	120	15	39	0	5
3	1		2	68	9	76	0	5
3	1		3	60	5	51	0	0
3	1		4	147	15	87	0	9
3	1	Jun	1	88	22	22	0	3
3	1		2	200	18	36	3	8
3	1		3	41	9	23	0	5

APPENDIX. Continued.

Station	Year	Month	Replicate	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*
3	1		4	386	36	95	1	15
3	1	Jul	1	1065	51	83	1	42
3	1		2	1527	100	94	1	78
3	1		3	868	89	79	3	68
3	1		4	288	89	80	3	51
3	1	Aug	1	460	75	42	0	17
3	1		2	541	105	109	6	43
3	1		3	185	52	49	0	12
3	1		4	803	65	127	8	29
3	1	Sep	1	475	110	112	0	23
3	1		2	341	29	40	0	28
3	1		3	448	24	56	1	18
3	1		4	384	25	47	0	9
3	1	Oct	1	727	35	80	4	9
3	1		2	51	15	23	1	5
3	1		3	44	8	7	1	1
3	1		4	274	19	37	2	5
3	1	Nov	1	39	0	12	0	0
3	1		2	21	3	7	0	0
3	1		3	11	11	7	0	1
3	1		4	20	9	14	0	0
3	1	Dec	1	35	3	20	0	2
3	1		2	74	13	31	5	1
3	1		3	9	3	8	0	0
3	1		4	47	7	20	0	0
3	1	Jan	1	158	25	79	1	12
3	1		2	55	5	28	4	3
3	1		3	27	14	21	2	2
3	1		4	68	19	57	2	4
3	2	Feb	1	294	67	61	3	10
3	2		2	167	6	74	0	10
3	2		3	63	5	30	0	9
3	2		4	133	18	65	0	4
3	2	Mar	1	20	1	6	0	3
3	2		2	168	22	99	3	12
3	2		3	199	34	79	1	12
3	2		4	60	20	51	0	14
3	2	Apr	1	80	15	41	0	10
3	2		2	64	17	64	1	3
3	2		3	172	39	141	1	11
3	2		4	80	19	60	1	5
3	2	May	1	128	15	21	1	5
3	2		2	97	7	28	1	2
3	2		3	72	2	30	0	3
3	2		4	215	13	39	0	2
3	2	Jun	1	201	11	9	0	3
3	2		2	526	37	40	1	19
3	2		3	450	5	15	0	48
3	2		4	689	16	29	1	34
3	2	Jul	1	552	32	29	2	52
3	2		2	656	14	28	2	21
3	2		3	454	21	13	1	24
3	2		4	258	10	9	0	11
3	2	Aug	1	63	2	5	0	0
3	2		2	20	2	11	0	0
3	2		3	46	1	7	0	3
3	2		4	13	2	2	0	2
3	2	Sep	1	325	12	17	0	18
3	2		2	805	45	58	1	34
3	2		3	232	16	31	0	16
3	2		4	394	24	30	1	22
3	2	Oct	1	254	9	89	2	23
3	2		2	124	6	20	0	7
3	2		3	194	23	53	1	9
3	2		4	83	5	15	0	3
3	2	Nov	1	285	12	42	4	5
3	2		2	343	10	37	3	10
3	2		3	181	15	27	3	5
3	2		4	240	14	41	3	5
3	2	Dec	1	181	11	49	1	12
3	2		2	81	3	33	1	7

APPENDIX. Continued.

Station	Year	Month	Replicate	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*
3	2		3	89	3	25	1	9
3	2		4	143	14	21	1	13
3	2	Jan	1	136	24	23	0	11
3	2		2	103	22	47	3	17
3	2		3	202	11	41	2	11
3	2		4	81	4	38	1	9
3	3	Feb	1	78	3	27	0	4
3	3		2	132	11	44	0	11
3	3		3	65	9	33	1	12
3	3		4	143	6	51	1	4
3	3	Mar	1	127	15	24	2	6
3	3		2	63	6	99	1	10
3	3		3	162	24	122	0	18
3	3		4	34	5	47	0	2
3	3	Apr	1	70	9	28	0	7
3	3		2	88	13	20	0	2
3	3		3	352	40	115	0	29
3	3		4	170	21	54	0	13
3	3	May	1	70	31	114	0	40
3	3		2	37	13	63	1	33
3	3		3	56	19	59	1	32
3	3		4	76	10	38	0	8
3	3	Jun	1	389	9	13	0	16
3	3		2	386	63	30	1	17
3	3		3	438	24	14	0	30
3	3		4	214	3	5	0	1
3	3	Jul	1	1100	24	60	2	27
3	3		2	929	58	69	1	50
3	3		3	483	40	48	0	15
3	3		4	905	49	25	0	47
3	3	Aug	1	534	40	43	1	63
3	3		2	541	43	37	3	25
3	3		3	574	20	38	0	31
3	3		4	982	32	42	0	78
3	3	Sep	1	130	11	14	0	4
3	3		2	25	3	2	0	0
3	3		3	33	0	9	0	4
3	3		4	296	19	24	0	4
3	3	Oct	1	322	16	14	0	11
3	3		2	352	16	26	1	13
3	3		3	464	17	58	0	16
3	3		4	188	6	34	0	7
3	3	Nov	1	123	26	69	1	6
3	3		2	159	41	83	1	8
3	3		3	237	59	65	3	10
3	3		4	173	42	72	1	10
3	3	Dec	1	54	45	53	2	11
3	3		2	43	31	57	1	10
3	3		3	111	51	77	1	8
3	3		4	177	37	85	2	24
3	3	Jan	1	56	28	53	1	13
3	3		2	65	15	12	0	11
3	3		3	28	30	41	1	22
3	3		4	101	74	51	0	12
3	4	Feb	1	36	33	28	1	14
3	4		2	13	23	22	1	12
3	4		3	52	40	45	0	6
3	4		4	21	17	31	0	18
3	4	Mar	1	81	56	139	0	27
3	4		2	75	79	77	0	54
3	4		3	70	40	63	0	36
3	4		4	20	15	47	0	19
3	4	Apr	1	422	78	231	3	28
3	4		2	351	103	176	3	24
3	4		3	778	152	250	0	17
3	4		4	236	55	142	2	5
3	4	May	1	895	129	267	5	111
3	4		2	33	19	18	0	5
3	4		3	414	83	197	5	74
3	4		4	133	64	57	0	13
3	4	Jun	1	754	67	113	4	68
3	4		2	394	90	108	1	56

APPENDIX. Continued.

Station	Year	Month	Replicate	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*
3	4		3	1556	130	127	6	316
3	4		4	813	93	28	0	86
3	4	Jul	1	378	60	96	2	57
3	4		2	376	33	93	3	47
3	4		3	211	27	80	1	30
3	4		4	381	42	67	1	30
3	4	Aug	1	197	27	47	0	36
3	4		2	156	17	22	0	19
3	4		3	307	18	40	0	87
3	4		4	705	83	134	1	231
3	4	Sep	1	109	16	27	1	4
3	4		2	183	48	41	0	23
3	4		3	166	39	37	0	15
3	4		4	145	50	28	1	11
3	4	Oct	1	220	46	49	1	12
3	4		2	164	44	48	0	12
3	4		3	101	17	13	0	9
3	4		4	158	44	21	0	18
3	4	Nov	1	161	48	125	0	15
3	4		2	212	96	43	2	21
3	4		3	147	24	53	1	10
3	4		4	131	22	25	0	7
3	4	Dec	1	340	24	54	1	12
3	4		2	319	20	69	1	8
3	4		3	77	11	27	0	5
3	4		4	47	1	9	0	0
3	4	Jan	1	62	23	29	1	1
3	4		2	15	5	4	0	8
3	4		3	31	9	17	1	9
3	4		4	68	7	30	0	18
3	5	Feb	1	37	3	15	0	9
3	5		2	68	31	54	0	58
3	5		3	181	42	67	0	32
3	5		4	105	29	49	2	29
3	5	Mar	1	184	36	93	0	26
3	5		2	87	18	33	1	10
3	5		3	127	19	46	1	8
3	5		4	56	5	45	0	5
3	5	Apr	1	53	10	19	0	3
3	5		2	129	30	47	0	16
3	5		3	90	12	54	0	13
3	5		4	64	17	63	0	6
3	5	May	1	240	5	36	0	6
3	5		2	286	6	22	0	15
3	5		3	240	5	26	0	7
3	5		4	219	5	47	0	5
3	5	Jun	1	421	7	25	0	3
3	5		2	636	121	15	1	5
3	5		3	201	14	12	0	4
3	5		4	366	29	22	2	3
3	5	Jul	1	85	1	19	0	3
3	5		2	122	2	16	0	1
3	5		3	416	13	40	2	4
3	5		4	886	43	49	3	2
3	5	Aug	1	506	2	55	1	5
3	5		2	747	16	90	0	11
3	5		3	772	46	140	3	20
3	5		4	749	23	44	0	9
3	5	Sep	1	447	29	52	1	20
3	5		2	529	31	55	0	17
3	5		3	383	13	37	1	16
3	5		4	926	38	65	4	16
3	5	Oct	1	255	8	54	0	2
3	5		2	315	10	62	2	11
3	5		3	304	11	40	0	4
3	5		4	316	12	56	1	6
3	5	Nov	1	287	6	44	2	4
3	5		2	272	9	40	0	10
3	5		3	259	11	35	0	4
3	5		4	490	15	58	0	10
3	5	Dec	1	145	2	16	1	1

APPENDIX. Continued.

Station	Year	Month	Replicate	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*
3	5		2	175	9	69	1	1
3	5		3	51	1	17	4	3
3	5		4	127	6	33	5	6
3	5	Jan	1	16	1	8	0	3
3	5		2	53	6	15	2	1
3	5		3	21	3	12	6	3
3	5		4	78	3	14	1	2